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Prairie grouse and wind energy: The state of the science and implications for risk assessment

John D. Lloyd[1] | Cameron L. Aldridge[2] | Taber D. Allison[1] | Chad W. LeBeau[3] | Lance B. McNew[4] | Virginia L. Winder[5]

[1]Renewable Energy Wildlife Institute, 1900 K St NW, Washington, D.C 20006, USA

[2]U.S. Geological Survey, 2150 Centre Avenue, Fort Collins, CO 80526, USA

[3]Western EcoSystems Technology, Inc., 1610 Reynolds St., Laramie, WY 82072, USA

[4]Department of Animal and Range Sciences, Montana State University, 211 Animal Bioscience Building, Bozeman, MT 59717, USA

[5]Department of Biology, Benedictine College, 211 Westerman Hall, Atchison, KS 66002, USA

Correspondence

John D. Lloyd, Renewable Energy Wildlife Institute, Washington, DC 20006.
Email: john.lloyd@outlook.com

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Abstract

How to shape the anticipated build-out of industrial-scale renewable energy in a way that minimizes risk to wildlife remains contentious. The challenge of balancing wildlife conservation and decarbonization of the electricity sector is well illustrated in the grasslands and shrub-steppe of North America. Here, several endemic species of grouse are the focus of intensive, long-term conservation action by a host of governmental and nongovernmental entities, many of whom are now asking whether anticipated increases in the number of wind-energy facilities will exacerbate declines or prevent recovery of these species. To address this question, we synthesized the potential consequences of wind-energy development on prairie grouse. Published literature on behavior or demography of prairie grouse at wind-energy facilities is sparse, with studies having been conducted at only 5 different facilities in the United States. Only 2 of these studies met the standard for robust impact analysis by collecting pre-construction data and using control sites or gradient designs. Only one species, greater prairie chicken, had published results available for >1 facility. Most (10/12) studies also drew conclusions based on short (<4 years) periods of study, which is potentially problematic when studying highly philopatric species. Given these caveats, we found that, in the short-term, adult survival and nest success appear largely unaffected in populations exposed to wind-energy facilities. However, changes in habitat use by female greater sage-grouse and female greater prairie-chicken during some seasons and reduced lek persistence among male greater prairie-chickens near wind turbines suggest behavioral responses that may have demographic consequences. Prairie grouse can coexist with wind-energy facilities in some cases, at least in the short term, but important uncertainties remain, including the potential for long-term, cumulative effects of the extensive development expected as states attempt to meet goals for generating electricity from renewable sources.

KEYWORDS

anthropogenic structures, *Centrocercus urophasianus*, greater prairie-chicken, greater sage-grouse, lesser prairie-chicken, sharp-tailed grouse, *Tympanuchus cupido*, *Tympanuchus pallidicinctus*, *Tympanuchus phasianellus*, wind energy

Electricity generation is one of the leading sources of greenhouse-gas emissions and decarbonization of this sector is a critical part of efforts to limit anthropogenic climate change (Bruckner et al. 2014, Rogelj et al. 2018). Reducing the severity of anthropogenic climate change by avoiding future emissions from fossil-fuel combustion is expected to yield significant long-term benefits for wildlife (Warren et al. 2018), whereas failure to address climate change is likely to lead to widespread wildlife extinctions (Wiens 2016). Renewable energy sources can contribute to reducing emissions of greenhouse gases; however, development of wind and solar facilities may also have adverse effects on some wildlife species (Kuvlesky et al. 2007, Lovich and Ennen 2011, Smith and Dwyer 2016, Allison et al. 2019). Transitioning to systems of low-carbon energy generation that are sustainable requires, in part, understanding the consequences for wildlife, and how to mitigate any negative effects. With installed capacity of renewable energy expected to increase significantly by 2050, the time available to build the scientific basis for risk assessment and impact mitigation is short.

Experience suggests that reducing the risk of negative effects on wildlife populations from increased deployment of renewable energy is possible when informed by reliable empirical information. For example, 2 decades of research on wind energy and wildlife interactions has led to an improved ability to assess risk and, in some cases, to mitigate effects on raptors, other migratory birds, and bats (Allison et al. 2019). For groups of wildlife where the scientific foundation is less well-established, however, efforts at risk assessment and mitigation are more contentious as important stakeholders may disagree on the degree of risk involved in constructing new facilities. However, a shared understanding of the evidence, as identified by a systematic and objective scientific approach, can serve as an important starting point.

Based on a systematic review of published results from studies of European and North American grouse, including species associated with forests, grasslands, shrub-steppe, and sub-arctic tundra, Coppes et al. (2020) concluded that wind-energy infrastructure often induced behavioral changes among exposed individuals. Results of studies examining changes in vital rates or population size were inconclusive, in part due to the reliance on short-term, unreplicated, and uncontrolled experimental designs. Coppes et al. (2020) were not able to determine whether the effects of wind-energy infrastructure on grouse varied among biomes. For example, forest-dwelling grouse might be more sensitive because of the gross changes in physiognomy and connectivity caused by tree removal to create roads and space for other infrastructure, whereas grouse of open country might respond more strongly because of an inherent aversion to tall structures on an otherwise flat, open environment (Robel 2002, Pruett et al. 2009).

LeBeau et al. (2020*a*) conducted a quantitative meta-analysis of the effect of proximity to a wind turbine on behavior and demography of grouse that inhabit the grasslands and shrub-steppe of North America. No significant relationships were found between proximity to a turbine and survival, habitat selection, and abundance of grouse, although point estimates suggested weakly negative relationships (LeBeau et al. 2020*a*). Effect sizes (i.e., the expected strength of association between proximity to a wind turbine and behavioral or demographic variables) were largest for survival and habitat selection, and smallest for the relationship between abundance and proximity to a turbine.

In our review, we attempt to add additional detail to the findings of Coppes et al. (2020) and LeBeau et al. (2020*a*) and to elucidate more fully some of the outstanding questions identified by these authors. Our objective in doing so was to summarize what is known about the effects of wind energy on grouse and to identify key knowledge gaps that could be filled by future research. As with LeBeau et al. (2020*a*), we focused on the North American prairie grouse, defined here to include greater sage-grouse (*Centrocercus urophasianus*), 2 species of prairie-chicken (greater prairie-chicken [*Tympanuchus cupido*] and lesser prairie-chicken [*T. pallidicinctus*]), and sharp-tailed grouse (*T. phasianellus*; in particular, plains sharp-tailed grouse [*T. p. jamesi*] of the Great Plains and Columbian sharp-tailed grouse [*T. p. columbianus*] of the Great Basin and Columbia Plateau). We focused on these species because they were of high conservation concern, having exhibited long-term, extensive declines in abundance and distribution (Connelly et al. 1998, Aldridge and Brigham 2003, Johnson et al. 2011, Western Association of Fish and Wildlife Agencies 2015, Garton et al. 2016), and because all have geographic distributions that may experience significant amounts of wind-energy development in the coming decades (Figure 1). Furthermore, prairie grouse are often regarded as indicators of overall ecosystem health, and insight into how they respond to ongoing land-use change may prove useful in developing conservation strategies that enhance the resilience and integrity of temperate grasslands and shrub-steppe that they inhabit.

By focusing on species of temperate grassland and shrub-steppe, we avoid the difficulty highlighted by Coppes et al. (2020) in drawing inference about the effects of wind energy when responses are pooled across species inhabiting widely different biomes (i.e., forest, tundra, steppe, and grassland). At the same time, by adopting a qualitative approach to our analysis, we provide a holistic synthesis of existing research that complements the meta-analytic approach of LeBeau et al. (2020*a*), in which constraints on study inclusion required excluding some pertinent research and in which only a single metric of impact–distance to a turbine–could be addressed. We included in our review every study of wind-energy impacts on these 4 species published in peer-reviewed journals, with a focus on those studies that measured endpoints directly relevant to conservation, including survival and habitat selection. In addition, we included LeBeau et al.'s (2020*b*) preliminary report on their study of lesser prairie-chicken at a wind-energy facility because it was 1) reviewed by independent experts prior to publication and 2) provides the only publicly available description of a study examining impacts of wind energy on this species.

EFFECTS OF WIND ENERGY ON PRAIRIE GROUSE

We begin with a review of the potential mechanisms by which constructing and operating wind energy might induce changes in prairie-grouse behavior or population dynamics. We then survey the existing literature concerning wind energy and its effects on prairie grouse and their habitats in the United States and Canada, highlight key conclusions, and conclude by identifying a path forward that would improve our understanding of how prairie grouse respond to wind-energy development and inform future conservation actions. Our purpose in providing this synthesis is to outline the empirical basis for assessing risk associated with future wind-energy developments and inform future research that will enhance the scientific basis for conserving prairie grouse in the face of anticipated build-out of wind energy.

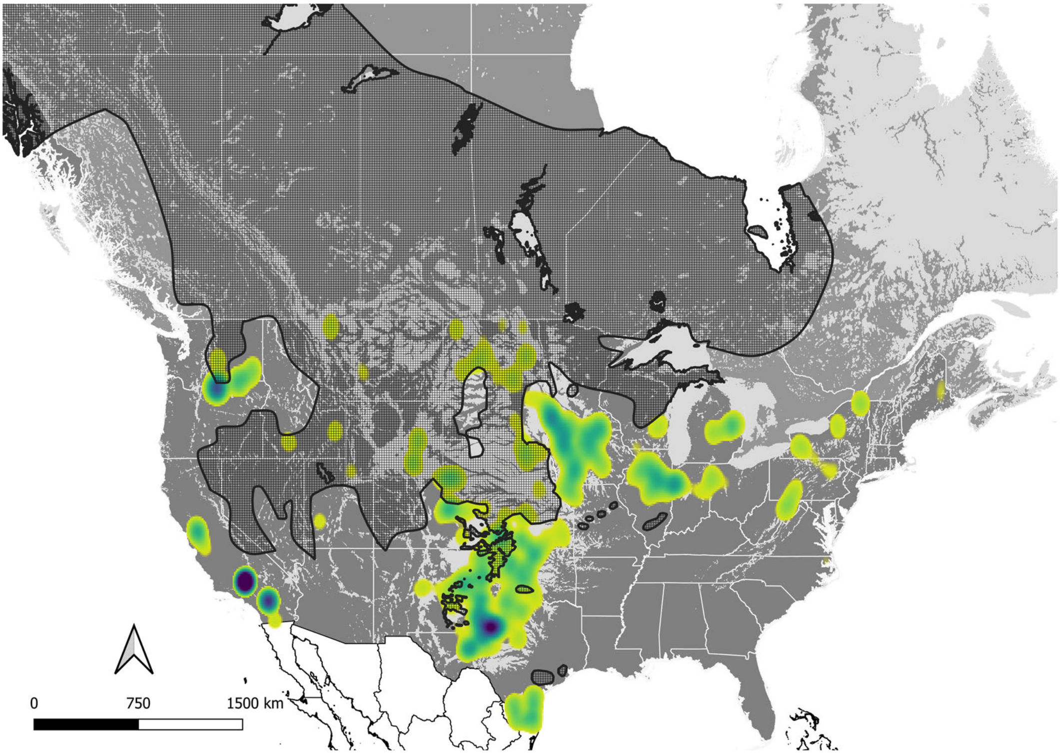

FIGURE 1 The collective distribution of greater sage-grouse (*Centrocercus urophasianus*), greater prairie-chicken (*Tympanuchus cupido*), lesser prairie-chicken (*T. pallidicinctus*), and sharp-tailed grouse (*T. phasianellus*; cross-hatched area; BirdLife International and Handbook of the Birds of the World 2019) overlap with areas supporting potentially important wind resources (light gray background are areas with wind speeds >7 m/s measured at 80 m above ground elevation). Highest densities of existing turbines (blue and green shading; estimated density of turbines based on data in Rand et al. 2020) are largely outside of the ranges of these species. Administrative boundaries are per GADM version 3.6 (http://www.gadm.org).

Anatomy of a wind-energy facility

Construction of wind-energy facilities typically involves building new access roads or improving existing roads, clearing sites on which to place turbines and associated infrastructure, and erecting service buildings and substations. Collection and delivery of power generated at the site may also require clearing areas for poles to support power lines or to dig trenches in which to bury power lines. The amount of land permanently occupied by wind-energy infrastructure is highly variable, ranging from 0.06–2.4 ha/megawatt (MW) with an average of 0.3 ha/MW (Denholm et al. 2009). For reference, the median capacity of facilities that began operating in 2019 was 201 MW (Rand et al. 2020). Differences in land cover—for example, forest versus agriculture—and topography at the facility location explain some of the variation in the extent of land-cover change associated with construction of a wind-energy facility (Diffendorfer and Compton 2014), with greater land transformation occurring at facilities built in steep, forested landscapes.

Roads account for most of the direct, permanent ground disturbance at wind-energy facilities in the United States (Denholm et al. 2009, Diffendorfer and Compton 2014). Turbine pads, substations, and transmission lines account for most of the remaining area of permanently disturbed land (Denholm et al. 2009). The area of land disturbed temporarily by construction, but not permanently occupied by infrastructure, is more extensive, averaging

0.7 ha/MW (Denholm et al. 2009). In addition to the temporary and permanent ground disturbance caused by wind-energy infrastructure, expanding renewable-energy generation will also demand construction of new transmission lines, which will result in additional land-cover change and additional fragmentation of habitat for prairie grouse. Although the exact amount of new transmission lines needed is difficult to predict, Larson et al. (2020) estimated that achieving net-zero carbon emissions economy-wide would require tripling the extent of existing high-voltage transmission lines, which currently measure approximately 386,000 km (Marston 2018). Importantly, although estimates of temporary and permanent changes in land cover provide one measure of the potential impacts of different forms of wind-energy infrastructure, the actual impact on biological receptors will likely depend not only on the area of land disturbed but also the nature of the disturbance itself–for example, noise or visual disturbance–and its interaction with local conditions such as topography.

Potential exposure of prairie grouse to existing wind-energy facilities

Based on overlap between the estimated range of each species (BirdLife International and Handbook of the Birds of the World 2019) and the location of all wind turbines in the United States (Wind Turbine Database version USWTDB_V4_0_20210409, available at https://eerscmap.usgs.gov/uswtdb/; Rand et al. 2020), approximately 17% of operating turbines fall within the range of one of the 4 species that we considered. Sharp-tailed grouse, with the most extensive geographic range, are exposed to the greatest number of turbines (5,004). Greater sage-grouse and greater prairie-chicken have fewer turbines within their geographic range (2,399 and 2,987, respectively), and the range of lesser prairie-chicken overlaps with an estimated 1,040 wind turbines. Note that our review ignored two additional taxa of prairie grouse, Gunnison's sage-grouse (*Centrocercus minimus*) and Attwater's prairie-chicken (*Tympanuchus cupido attwateri*), because they are not currently exposed to any wind-energy development.

Potential mechanisms of effect: how might wind-energy facilities affect behavior and demography of prairie grouse?

Construction and operation of wind-energy facilities may affect prairie-grouse populations by both direct and indirect pathways. We differentiated between direct and indirect effects using the approach of Hebblewhite (2011).

Direct effects

Direct effects of development are those that occur via the direct interaction of people, infrastructure, and the focal species, and may include habitat loss and degradation (e.g., due to noise; Blickley et al. 2012, Ortega 2012) or direct mortality caused by humans or infrastructure. Prairie grouse are vulnerable to collisions with fences and powerlines, and in some cases, collisions may form an important source of annual mortality (Beck et al. 2006, Wolfe et al. 2007, Stevens et al. 2012, Robinson et al. 2016). Existing evidence does not suggest that mortality from collisions with turbine blades or towers is widespread; the most comprehensive database of bird deaths at wind facilities, drawing from 230 monitoring studies conducted between 2000–2017 at 130 different facilities in the US, reported 4 carcasses of greater sage-grouse, 2 of sharp-tailed grouse, and one of greater prairie-chicken out of a total of 6,655 recorded fatality incidents (AWWI 2019).

Direct habitat loss from land-cover conversion is small and derives mostly from the area of new roads required to construct and service turbines. Habitat may also become inaccessible in areas where fencing is required for safety or security reasons. Potentially more important than habitat loss from land-cover change is the functional habitat loss that occurs if individuals avoid using otherwise available habitat around wind-energy infrastructure.

Importantly, functional habitat loss occurs even in the absence of changes to land cover. In general, the avoidance behavior underlying functional habitat loss is thought to be a response to changes in the perceived risk of predation, which itself is presumably driven by some visual or acoustic cue associated with wind-energy infrastructure or associated activities (Frid and Dill 2002). For example, Pruett et al. (2009) argued that a cognitive association between tall objects and avian predators might trigger avoidance of wind turbines that would lead to functional habitat loss. Indeed, during long-distance dispersal, lesser prairie-chickens stayed further away from taller structures such as transmission lines and towers than from other forms of infrastructure (Peterson et al. 2020). However, isolating infrastructure height as the causal agent driving avoidance responses by prairie grouse remains challenging (Walters et al. 2014).

Other cues associated with increased human activity, including vehicular traffic, construction noise, or noise produced by turbines during operation, might generate a similar response, as has been suggested to explain avoidance of roads and oil and natural-gas wells by greater sage-grouse (Blickley et al. 2012, Fedy et al. 2015, Holloran et al. 2015). Greater prairie-chickens at leks closer to wind turbines at a facility in Nebraska exhibited changes in vocalizations that may have been caused by noise produced by the turbines, or the roads built to service them (Whalen et al. 2018). Some of the observed changes in vocalizations were consistent with males attempting to minimize the masking effect of background noise, which suggests some ability to compensate for added noise (Whalen et al. 2018). However, if adjustments in behavior are energetically more expensive, or place individuals at greater risk of predation, then compensation for added noise may come with costs. In some cases, compensation may be impossible, and noise associated with wind-energy infrastructure might mask vocalizations that attract females to leks, potentially leading to lek abandonment (Raynor et al. 2017, Whalen et al. 2019). The effect of background noise is expected to be most significant at leks attended by few individuals (Raynor et al. 2017) and thus even if noise is not a primary driver of demographic change it could exacerbate declines caused by habitat loss or degradation.

Avoidance behavior underlying functional habitat loss reduces the carrying capacity of an area in the same way as would actual habitat loss or degradation, being mediated ultimately by some form of density-dependent reduction in recruitment or survival. However, measurable effects on vital rates and population abundance may take longer to manifest and be more difficult to estimate given the sample sizes typical of most studies of prairie grouse (e.g., Winder et al. 2014*b*, $n = 220$; LeBeau et al. 2017*a*, $n = 346$). Changes in patterns of habitat selection that are indicative of avoidance may arise more quickly and be more readily detectable but must translate into demographic changes if they are to produce population-level consequences and thus prove relevant for conservation. Coupled patterns of avoidance, isolation, diminished vital rates, and ultimately population decline are apparent from studies of prairie grouse responses to other forms of energy development, such as transmission lines (Aldridge and Boyce 2007, Holloran et al. 2010, Gibson et al. 2018, LeBeau et al. 2019).

Indirect effects

Indirect effects are those mediated by changes in the abundance or activity of other species, especially predators, which are in turn associated with operation and construction of wind-energy facilities (Hebblewhite 2011). Indirect effects could arise through changes in the risk of predation by increases in predator abundance or activity (e.g., edge effects leading to lower nest survival) or through associated changes in behavior of prairie grouse (e.g., predator avoidance). Indirect effects on prairie grouse could be positive, too, if predators were to avoid wind-energy facilities. For example, Smith et al. (2016) suggested that male greater prairie-chickens at leks closer to wind turbines might spend less time engaged in anti-predator behavior because raptors avoided areas around turbines. The only published study to examine the potential effects of a wind-energy development on predators of prairie-grouse found no evidence that occupancy rates of potential predators varied as a function of distance to a turbine (Smith et al. 2017). Studies of other forms of energy development, including oil fields, suggest that indirect effects may be important (Lockyer et al. 2013, Coates et al. 2014, Dinkins et al. 2014, Burr et al. 2017, Gibson et al. 2018).

Studies at wind-energy facilities: research design

Research on prairie-grouse population ecology has been carried out at 5 different wind-energy facilities, with only one species—greater prairie-chicken—having been studied at more than one location (Table 1). No published studies have evaluated the effects of wind-energy development on plains sharp-tailed grouse. Although all studies used some form of control, most often a gradient design, only 2 facilities have hosted studies that collected pre-construction data. This reflects in large part the difficulty of obtaining funding for the collection of pre-construction data; many proposed wind projects are abandoned before construction begins, which makes investing in preconstruction data collection a risky and unappealing prospect for funders and investigators. Nonetheless, pre-construction data at both developed and associated undeveloped areas are critical to separating regular spatial-temporal variation in space use and demography from impacts of energy development (Anderson et al. 1999, Powell et al. 2017). Moving forward, a key challenge for all stakeholders will be to develop and implement, through incentives or regulations, collaborative systems for financing universal collection of pre-construction data. LeBeau et al. (2017*b*) used an unreplicated Before-After/Control-Impact (BACI) design, with control data collected at a site adjacent to the wind facility but far enough from the turbines ($\bar{x}$ distance from control leks to a turbine = 11.0 km, min-max = 7.1–16.2 km) to be considered independent of any treatment effect. McNew et al. (2014) and Winder et al. (2014*a*, *b*; 2015) paired a gradient design (Morrison et al. 2008), in which effects are assessed using the response of individuals measured at different distances from the wind turbines, with a before-after framework (i.e., a before-after/gradient [BAG] design). The length of the gradient for these 4 studies, or distance over which effects were measured, was approximately 28 km. Studies at the 3 other wind facilities that have hosted research have not had pre-construction data.

TABLE 1 Summary of studies that have examined wind-energy effects on behavior and demography of North American prairie grouse.

State	No. turbines (total capacity)	Species	Landscape context	Experimental design	Before/after years of data collection
Wyoming	79 (118.5 megawatts [MW])	Greater sage-grouse	Intact sage-steppe	Before-After/Control-Impact[a] After/Control-Impact[b] After/Gradient[c]	3/8 0/6 0/2
Idaho	215 (366.3 MW)	Sharp-tailed grouse	Fragmented Palouse prairie, crop	After/Gradient[d]	0/2
Kansas	67 (201 MW)	Greater prairie-chicken	Fragmented tallgrass prairie, crop	Before-After/Gradient[e,f,g,h]	2/3
Nebraska	36 (59.4 MW)	Greater prairie-chicken	Intact tallgrass prairie	After/Gradient[i,j,k]	0/2
Kansas	200 (400 MW)	Lesser prairie-chicken	Fragmented mixed-grass prairie, crop	After/Gradient[l]	0/3

Source for experimental design: [a]LeBeau et al. 2017*b*; [b]LeBeau et al. 2017*a*; [c]LeBeau et al. 2014; [d]Proett et al. 2019; [e]McNew et al. 2014; [f]Winder et al. 2014*a*; [g]Winder et al. 2014*b*; [h]Winder et al. 2015; [i]Harrison et al. 2017; [j]Smith et al. 2017; [k]Raynor et al. 2019; [l]LeBeau et al. 2020*b*.

Studies at wind-energy facilities: evidence for effects

Research on the effects of wind energy on prairie grouse have focused on 2 general endpoints: individual vital rates and patterns of behavior. Studies estimating associations between vital rates and wind-energy infrastructure have considered adult survival, brood survival, and nest survival. No research has yet addressed recruitment, comprehensive measures of individual fitness, or changes in population growth rate. Studies examining changes in behavior have focused on patterns of habitat selection during the breeding season, in particular male selection of leks and female selection of nesting and brood-rearing habitat. Effects of wind-energy infrastructure on habitat use outside of the breeding season have been examined only for greater prairie-chicken (Winder et al. 2014*a*) and lesser prairie-chicken (LeBeau et al. 2020*b*).

Adult survival

Survival of adult female greater prairie-chicken (Winder et al. 2014*b*, Smith et al. 2017), greater sage-grouse (LeBeau et al. 2014, LeBeau et al. 2017*a*), and lesser prairie-chicken (LeBeau et al. 2020*b*) did not vary as a function of distance to a wind turbine. Although the aforementioned studies included survival estimates from a fairly wide range of time intervals post-construction (e.g., Winder et al. 2014*b* measured survival in the first 3 years after construction, whereas Smith et al. 2017 measured survival 8 and 9 years after construction), all were derived from relatively short time-series (i.e., 2–3 years; the 6-year time series in LeBeau et al. 2017*a* was the longest).

Several studies reported a positive effect of wind-energy facilities on adult female survival: Winder et al. (2014*b*) found that annual survival of greater prairie-chickens was substantially greater during the 3-year post-construction period than the 2-year pre-construction period (57% v. 32%), and LeBeau et al. (2017*a*, 2019) found survival of greater sage-grouse and lesser prairie-chicken was greater in areas that contained a higher density of wind-energy infrastructure (roads and turbine pads). Explanations for higher post-development survival are speculative but generally involve potential negative effects of development on common predators of prairie grouse (i.e., a positive indirect effect on grouse; Winder et al. 2014*b*, LeBeau et al. 2017*a*, Smith et al. 2017). Evidence that wind-energy facilities support altered predator assemblages is, however, lacking (Smith et al. 2017).

Reproduction

Nest survival for greater prairie-chicken was not affected by the development of a 201-MW wind-energy facility (McNew et al. 2014). Harrison et al. (2017) and Proett et al. (2019) found no relationship between distance to a wind turbine and nest survival of greater prairie-chicken and sharp-tailed grouse, respectively, but did not collect pre-construction data and thus it remains uncertain whether patterns of nest survival were affected by construction and operation of the facilities at which they worked. LeBeau et al. (2014) reported that survival of greater sage-grouse nests and broods declined with proximity to a wind turbine (nest survival declined 7.1% with every 1-km increase in proximity to a turbine; brood survival declined 38.1% with every 1-km increase in proximity to a turbine). However, an analysis of a larger sample from a longer time-series collected at the same facility found no effect of distance to a wind turbine on either nest or brood survival (LeBeau et al. 2017*a*). These contrasting findings from the same location highlight the challenges associated with drawing conclusions about prairie-grouse demography from samples collected over short time periods. In addition, although the preponderance of evidence indicates no deleterious effects of wind-energy development on nest survival, the lack of pre-construction data (except for McNew et al. 2014) hinders our ability to draw definitive conclusions.

Abundance and habitat use

Winder et al. (2015) found no significant effect of proximity to a turbine on the probability of greater prairie-chicken lek persistence nor any differences in the probability of pre- and post- construction lek persistence when the study area was considered as a whole. Number of males attending leks was also unaffected by construction and operation of the wind-energy facility. However, when a subset of leks within 8 km of a turbine were analyzed separately, persistence was lower for leks closer to turbines. The decline in probability of persistence was steepest within approximately 3 km of a turbine. Among greater sage-grouse, LeBeau et al. (2017*b*) found no effect of a 118.5-MW wind-energy facility on trends in the number of males attending leks from pre- to post-development within a control and treatment area.

Nest-site selection by greater prairie-chicken, sharp-tailed grouse, greater sage-grouse, and lesser prairie-chicken was unaffected by wind turbines, suggesting vegetation structure at this scale of habitat selection is more influential than the presence of wind energy infrastructure (McNew et al. 2014, Harrison et al. 2017, LeBeau et al 2017*a*, Proett et al. 2019, LeBeau et al. 2020*b*). At larger spatial scales, patterns of habitat use by male and female lesser prairie-chickens at a site in Kansas were unrelated to the presence of wind turbines (LeBeau et al. 2020*b*). Female greater prairie-chickens in Kansas were not displaced by construction of a wind-energy facility but, following construction, tended to increase use of those parts of their breeding-season home range that were farther from turbines (Winder et al. 2014*a*). Space use during the non-breeding season was not affected by construction and operation of the facility. Average home-range size also increased following construction, suggesting a real or perceived decline in habitat quality. Raynor et al. (2019) did not find a relationship between distance to a turbine and relative probability of space use or habitat selection during the breeding season among female greater prairie-chickens at a site in Nebraska, although the lack of pre-construction data hinders interpretation of this result. LeBeau et al. (2017*a*) found that areas with a greater proportion of land disturbed by infrastructure at a wind-energy facility were less likely to be used by female greater sage-grouse during brood-rearing and post-brood-rearing periods. Avoidance of wind-energy infrastructure was stronger in the later years of the study, suggesting a lag time in response of at least 3 years.

Studies at wind-energy facilities: data limitations

Five key limitations characterize existing research. First, despite the consensus that replication of study results is critical to progress in any field, including wildlife biology (Johnson 2002, Nichols et al. 2019), replication of studies examining interactions between prairie grouse and wind energy at different facilities is lacking. Second, most studies lack pre-construction data, meaning that estimates of effect are valid only if distributions of response variables—survival, reproductive success, or habitat selection—in control and treatment areas differ solely due to the presence of wind turbines, or if those effects can be isolated statistically. Wind-energy facilities are not located randomly within a landscape, and thus it is likely that a whole suite of environmental factors, some related to the facility and some not, will vary with distance to a turbine. Without pre-construction data, it can be difficult or impossible to account for such factors.

Third, most studies base inference on short time-series, yet short-term responses to wind-energy development may not provide insight into long-term consequences. Indirect effects mediated by changes in habitat may take years to manifest in the form of altered vital rates and population-level responses, and site fidelity may delay the appearance of avoidance behavior. Exactly how long studies should extend is uncertain, but studies of impacts of oil and gas development on prairie grouse suggest that time lags of approximately 4 years are common (Walker et al. 2007, Carpenter et al. 2010, Doherty et al. 2010, Gregory and Beck 2014, Green et al. 2017). However, some effects may take as long as 10 years to manifest (Harju et al. 2010). The complexity of identifying lagged responses is compounded by the cyclical nature of many grouse populations.

Fourth, existing research has focused on turbine proximity as an index of the expected magnitude of impact, yet proximity is at best an incomplete measure (LeBeau et al. 2020*b*). Overall extent of surface disturbance may be more important (Kirol et al. 2020). For example, the deleterious effects of oil and gas development tend to increase with well density (Doherty et al. 2008, Green et al. 2017) and in some cases are only detectable after a certain threshold of well density is passed (Doherty et al. 2010, Harju et al. 2010). Construction of wind-energy facilities may result in direct loss of habitat and habitat fragmentation at extents comparable to those associated with oil and gas extraction (Jones and Pejchar 2013), suggesting that future studies should account not just for proximity to a turbine, but also the density of wind-energy infrastructure on the landscape. It also highlights the need for caution in predicting the cumulative effects of wind-energy build-out (i.e., a density effect) from studies examining responses of local populations to individual wind-energy facilities (i.e., a proximity effect).

Finally, causal mechanisms underlying variation in the response of prairie grouse remain unexplored. The lack of insight into cause-and-effect relationships between prairie grouse and wind-energy infrastructure is in part related to the lack of pre-construction data. Wind-energy facilities are not simply the towers and turbines; they may include or be co-located with new or existing road networks, buildings, and powerlines, implying not only additive but potentially interactive effects of complex patterns of land-use and development on grouse populations. To which of these can we attribute behavioral or demographic responses? Is it the tall structures? The road traffic and vehicle noise? Without pre-construction data, and without an explicit consideration of them in the study design, the influence of these individual components of infrastructure are not easily distinguished. Roads can contribute to functional habitat loss for all species of prairie grouse (Pitman et al. 2005, Hagen et al. 2011, McNew et al. 2013, Harrison et al. 2017). Prairie grouse are less likely to use otherwise available habitat near power lines (Pitman et al. 2005, Hagen et al. 2011, Plumb et al. 2019), and populations near power lines tend to have lower reproductive success (Pitman et al. 2005, Gibson et al. 2018, Kohl et al. 2019), lower apparent adult survival (LeBeau et al. 2019), and higher probability of extirpation (Wisdom et al. 2011). Collisions with power lines can be a significant source of mortality in some locations (Beck et al. 2006, Wolfe et al. 2007). Despite the difficulty in doing so, decomposing the response of prairie grouse to different elements of the overall infrastructure of a wind-energy facility would inform efforts to both avoid and minimize impacts. At the same time, a focus on understanding the impacts of specific elements of wind-energy infrastructure should not come at the cost of delaying much-needed research into the potential significance of the cumulative effects of increased total density of infrastructure on the landscape.

CONCLUSIONS

Studies conducted to date suggest variable responses among prairie grouse to the construction and operation of wind-energy facilities. In some cases, prairie grouse appear to avoid areas around wind-energy infrastructure. In others, no evidence of avoidance or displacement was found. When it occurred, avoidance of habitat near wind-energy infrastructure was most apparent among males attending leks and among females during the breeding season, especially during the brood-rearing period. Heightened sensitivity to human disturbance during the breeding season has been reported previously (Hagen 2010, Hovick et al. 2014). Vital rates were not depressed by the construction or operation of wind-energy facilities, at least over the short timescales considered thus far. Indeed, several studies reported positive changes in adult and nest survival among individuals using habitat found within wind-energy facilities.

Heterogeneity in the response of individuals and populations to wind-energy development is consistent with previous analyses of the effects of renewable energy on wildlife (Smith and Dwyer 2016, Coppes et al. 2020). It is also consistent with studies of how prairie grouse respond to other forms of infrastructure. For example, although roads, powerlines, and oil and gas development may have negative effects on survival and habitat use of prairie grouse (Hagen 2010, Hovick et al. 2014, Peterson et al. 2020), the magnitude of these effects and distance at which they are detectable is highly variable among species and locations (see also Northrup and Wittemyer 2013, Gregory and Beck

2014, Manier et al. 2014). Variation among studies in how prairie grouse respond to infrastructure implies a significant degree of context-dependency, wherein the effects of any particular disturbance will depend on a host of idiosyncratic biotic and abiotic factors. Site- and species-specific responses may preclude ever developing a universal framework for predicting impacts of any given development, but research that improves our understanding of the causes of variation —which is lacking at present—would prove useful in identifying low-impact pathways to a decarbonized energy sector. We suggest reframing the critical research question from what are the impacts of wind-energy on prairie grouse to what drives variation, among individuals and populations, in the response to wind-energy development; our review of the science suggests that the former can only be answered conditionally.

Context dependency challenges not only our ability to understand ecological processes but also to implement effective conservation measures. Site- and species-specific variation in the response to wind-energy facilities implies that measures (e.g., setbacks or buffers) useful in protecting one population may prove inadequate or overly restrictive when applied to another. Until we can better predict the conditions that underlie this heterogeneity, wind-energy development that occurs within areas occupied by prairie grouse will best promote conservation of these species by evaluating projects on a case-by-case scenario and by using long-term monitoring to inform adaptive management and improve impacts assessments of future projects.

With the emerging consensus regarding the need to reduce greenhouse-gas emissions over the next decade (Intergovernmental Panel on Climate Change 2019), pressure to increase the deployment of renewable energy sources like wind will only become more intense. To do so while conserving populations of prairie grouse will require a coordinated effort to link research, monitoring, and management that treats every new wind-energy development as an opportunity to test hypotheses and refine mitigation approaches.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Our study did not involve live animal subjects. No permits or permissions were required for the research reported here.

ORCID

John D. Lloyd http://orcid.org/0000-0002-9143-3789

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